

RADIOLARIA FROM THE NAMURIAN OF DERBYSHIRE

by B. K. HOLDSWORTH

ABSTRACT. *Albaillella pennata* sp. nov. and *Popofskyellum undulatum* Deflandre are described from calcareous concretions at the horizon of the goniatite *Reticloceras paucicrenulatum* Bisat and Hudson. The diagnosis of the genus *Albaillella* is emended. It is suggested that *A. pennata* and *P. undulatum* may possibly have been favoured by depths of water greater than those necessary for the proliferation of Namurian spumelline Radiolaria, and that depths favouring these two forms may have been attained only rarely during the deposition of Namurian goniatite bands in Derbyshire and Staffordshire.

THE occurrence of well-preserved Radiolaria associated with Namurian goniatites in North Staffordshire and South-west Derbyshire has been reported (Holdsworth 1964). The goniatites and Radiolaria are found in syndepositional calcite concretions—'bullions'—enclosed in shale, these bullions being closely comparable with the calcareous concretions of the Ohio Shale (Devonian) from which Foreman (1959, 1963) described rich radiolarian faunas.

The Namurian bullions appear to contain some of the best-preserved Carboniferous Radiolaria yet known, and other than the Ohio Shale occurrence, the faunas of some lower Viséan phosphatic nodules described by Deflandre (1946, 1952, 1958) and of some upper Viséan nodules (Demanet 1938), there are no records of Palaeozoic Radiolaria which can be studied in comparable detail. Palaeozoic Radiolaria are most commonly found in siliceous sediments and the faunas described only from thin-section studies (cf. Hinde 1899, Aberdeen 1940). Though the problem of separating the Namurian Radiolaria completely from the carbonate matrix has not been solved, nevertheless it has been possible to study many hundreds of excellent specimens on limestone surfaces etched with hydrochloric acid. In such preparations both external and internal structures can be determined more conveniently and with greater certainty than in thin-section.

Radiolarian faunas at sixteen successive goniatite horizons have been examined (cf. Holdsworth 1964), the zonal range being from low $E_2b.1$ to low R_2b , Arnsbergian Stage to mid-Marsdenian Stage, some two-thirds of the Namurian Series. The very great majority of the faunas are largely composed of spumelline forms belonging to the genera *Entactinia*, *Entactinosphaera*, and *Polyentactinia*. The detailed taxonomic work on these spumellines is still incomplete, but it seems clear that there is no obvious, regular change in species present from horizon to horizon comparable with the marked and irreversible trend of the successive goniatite faunas.

Differences which are seen between radiolarian faunas at different horizons, and between different collections from essentially the same horizon, are mainly ones of population density and of relative abundance of a few rather well-marked species. The form with the most notably fluctuating abundance, however, is the new species of the genus *Albaillella* (suborder Albaillellina) described below.

Non-spumelline Radiolaria are usually rare members of the Namurian faunas. *Albaillella pennata* sp. nov. has been found only at the horizon of *Reticuloceras paucicrenulatum* Bisat and Hudson, being abundant in two collections from a single locality but absent in two other collections from different localities. A closely related form, *Albaillella* aff. *pennata*, occurs at the lower horizon of *Homoceras subglobosum* Bisat. *Popofskyellum undulatum* Deflandre is very sparsely associated with *A. pennata* at the horizon of *R. paucicrenulatum* but has not been seen elsewhere.

Both the genera *Albaillella* and *Popofskyellum* were first described from the Viséan of the Montagne Noire and Cabrière. Neither genus has previously been described from other levels, nor from any British rocks.

SYSTEMATIC DESCRIPTIONS

Subclass RADIOLARIA Müller 1858

Order PORULOSIDA Haeckel 1887

Suborder ALBAILLELLINA Deflandre 1953

Diagnosis. Fossil Radiolaria with bilaterally symmetrical, elongate, siliceous shells, having a thin and usually imperforate wall and possessing internally non-axial rays—‘columelles’ (columellae) of Deflandre—eventually merging with the shell wall. Outside the shell is developed a skeleton, variable in detail.

Remarks. Deflandre (1952) suggested that a new order should probably be created for the genus *Albaillella*, but did not erect the order Albaillellidea until the following year (1953a). The order was defined fully by Deflandre in 1958 (p. 2278) and his diagnosis is quoted above. The Albaillellids are omitted by Campbell and Moore (1954) from the Treatise on Invertebrate Paleontology, Part D (cf. Deflandre 1960, p. 214), but in the framework of the Treatise classification it appears that the group should be considered as constituting a suborder rather than an order. In relegating the Albaillellidea to a suborder the present writer follows Foreman (1963, p. 285). (In Foreman (loc. cit.) the words ‘Suborder Albaillellina ? Deflandre 1953’ should appear immediately above the line ‘Family Albaillellidae ? Deflandre 1952’ (Foreman *in litt.* 1964).)

Two families, Albaillellidae and Lapidopiscidae (Deflandre 1958), are included in the Albaillellina. Whilst recognizing a very broad similarity of form and structure between the Albaillellidae, type family of the Albaillellina, and the Cyrtioidea, Deflandre (1952) considered the bilateral symmetry of the Albaillellidae to exclude them from the Cyrtioidea and from the Nassellina as a whole. This total separation of Albaillellina and Nassellina is accepted here, but it may be noted that rudimentary bilateral symmetry is expressed in the sagittal ring and spicule arrangement of some simple members of the Nassellina (cf. Campbell, *in* Campbell and Moore 1954, fig. 8) and that there is at least some analogy, possibly even homology, between the H-frame of *Albaillella* (cf. Deflandre 1952, fig. 5) and the spicular structures of simple members of the Nassellina with complete, unisegmental lattice shells. In the absence of demonstrable homologies, however, the Albaillellids are best considered as a separate suborder.

Family ALBAILLELLIDAE Deflandre 1952

Diagnosis. Fossil Radiolaria with thin, conical, bilaterally symmetrical, lamellar shells. Shells built on a framework of which the principal part, formed by two longitudinal

rods of dissimilar strength joined by a curved transverse bar (the H-frame), is exterior to the shell and opposite the basal aperture.

Remarks. The most characteristic feature of the family is the externally developed H-frame. The only known genus is *Albaillella*, though Foreman (1963) tentatively referred *Ceratoikiscum* Deflandre and *Holoeciscus* Foreman to the family.

Genus ALBAILLELLA Deflandre 1952

Type species. *Albaillella paradoxa* Deflandre.

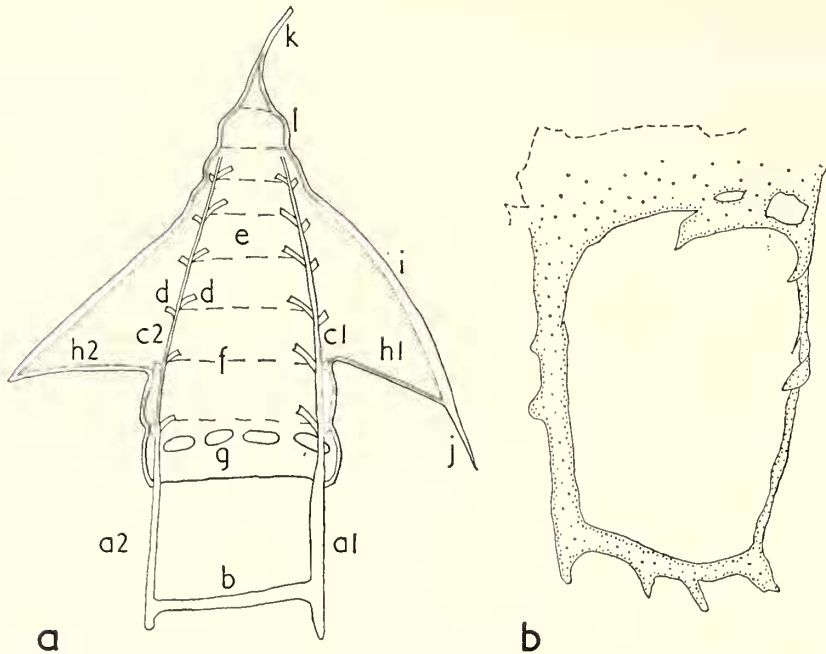
Emended diagnosis. Albaillellina in which the conical lattice shell may or may not be flattened bilaterally in the plane of the H-frame. Lattice shell may bear one or two hollow wings in the plane of the H-frame or may lack wings. Lattice shell sometimes shows a transverse segmentation or sometimes an oblique banding. Both rods of the external H-frame are produced into the interior of the lattice shell as longitudinal rays (columellae of Deflandre). They are of dissimilar strength, the stronger being developed from the stronger ray of the H-frame. The weaker (ventral) columella is sometimes indistinct. The stronger (dorsal) columella is usually attached to the inner surface of the lattice by paired lateral apophyses—'trabecules' (trabeculae) of Deflandre—and in some cases both rays are thus attached.

Remarks. Deflandre's several published accounts of forms attributed to *Albaillella* are not sufficiently detailed to establish the full variation encountered within the Viséan material with which he deals, or to decide how closely individual species agree with the original generic diagnosis. In the first publication on *Albaillella* (1952) a generic diagnosis is given, but no species names are mentioned in the text. Three species, *A. paradoxa*, *A. cornuata*, and *A. undulata*, and one variety, *A. paradoxa* var. *gibbosa*, are described only by drawings and named only in captions. The specific descriptions have not subsequently been amplified, though var. *gibbosa* was later given the status of a species (1960, p. 216, caption to pl. 1, fig. 23).

It is unclear from the published descriptions whether Viséan species of *Albaillella* invariably possess only a single columella—as appears to be the case in *A. paradoxa*, the type species (Deflandre 1952, p. 872, and fig. 4)—or whether both rods of the H-frame continue into the shell in the form of columellae, as is suggested by Deflandre (1953*b*, p. 408, fig. 307A, B). According to Deflandre (*in litt.* 1965) Viséan forms of the genus always, in fact, possess two columellae [as does the new Namurian species *pennata*] but the weaker (ventral) columella 'often shows a tendency to become effaced by inclusion in the shell wall'. Deflandre (*in litt.*) states that in Viséan species the stronger (dorsal) columella is 'often' attached to the shell wall by trabeculae, and that in 'some individuals' both dorsal and ventral columellae are so attached, the condition found in *A. pennata*. It should be noted that the columellae are simple continuations of the H-frame rods, not 'branches' from them as is suggested by the original description (Deflandre 1952, p. 872).

Clearly, the organization of the Namurian species is sufficiently similar to that of the Viséan forms for all to be included in a single genus. Apertural spines and an obliquely banded shell (cf. Deflandre 1953*b*, pp. 431–2) should not be considered as generic

features since they are not invariably present in Viséan species and are absent from the Namurian species.



TEXT-FIG. 1. *Albaillella pennata* sp. nov.

a, Diagrammatic representation of longitudinally bisected specimen to show the main architectural elements. *a1*, *a2*, dorsal and ventral rods of H-frame; *b*, cross-bar of H-frame; *c1*, *c2*, dorsal and ventral internal columellae; *d*, *d*, trabeculae; *e*, segment; *f*, constriction; *g*, pore; *h1*, *h2*, dorsal and ventral wings; *i*, wing rib; *j*, wing spine; *k*, apical spine; *l*, wall of lattice shell.

b, H-frame. Drawing from specimen, $\times 375$.

Anatomical nomenclature of Albaillella. The main architectural elements of frame and shell are illustrated diagrammatically in text-fig. 1. The side of the shell bearing the stronger columella is termed 'dorsal', as in the bicolumellate Lapidopiscidae (Deflandre 1958) which lack the H-frame. In *Albaillella pennata* the lattice shell is divided by transverse constrictions into a number of units and a similar, though less marked, partition of the lattice appears to be present in *A. undulata*. Each unit is here termed a 'segment', but the segmentation of the *Albaillella* lattice is not homologous with the segmentation in the Nassellina. In the Nassellina the first segment contains the spicular structures, if present, and these structures are thus isolated from all subsequent segments. Therefore, if the internal skeletal elements of the *Albaillella* are considered homologous with the spicular structures and sagittal ring of the Nassellina (see above), then the entire shell of *Albaillella* must be considered homologous with a single nasselline segment, comparable with the unisegmental lattice of the Archipiliidae.

The segmented lattice of *A. pennata* differs from the banded lattices (Deflandre 1952, p. 873; 1953b, p. 432) of *A. paradoxa* and *A. cornuata* in that the bands of these latter species are obliquely, not transversely, arranged. Thus portions of more than one band

are present at the periphery of the basal aperture in banded shells. In segmented shells the aperture is in a single segment.

The 'wings' of *A. pennata* are hollow portions of the lattice developed dorsally and ventrally, similar to the single outgrowth of the shell in *A. cornuata*, and differing from the 'horns' of *Lapidopiscum* (Deflandre 1958, p. 2279) in that they contain no portions of the columellae. It should be noted that Deflandre uses 'horn' in a quite different sense with respect to *Popofskyellum* (see below). In this case the horns are slender, solid, or hollow spines developed from the cephalis, not containing or continuous with columellae or spicules. These structures in *Popofskyellum* are therefore better termed simply 'cephalic spines'.

The outer margins of the wings in *A. pennata* are usually thickened to form longitudinal 'wing ribs' which may be produced beyond the tip of the wings as 'wing spines'. In his 'hypothetical reconstruction' of the *A. cornuata* frame Deflandre (1953*b*, fig. 307*A*) shows a lateral branch from the ventral columella in a position corresponding to the wing of *A. cornuata*. It is now known that there is no such connection between outgrowth and columella (Deflandre, *in litt.* 1965). The *A. cornuata* wing is comparable to the wings of *A. pennata* in that it is developed solely from the shell.

Albaillella pennata sp. nov.

Plate 54, figs. 1-3, 5-7

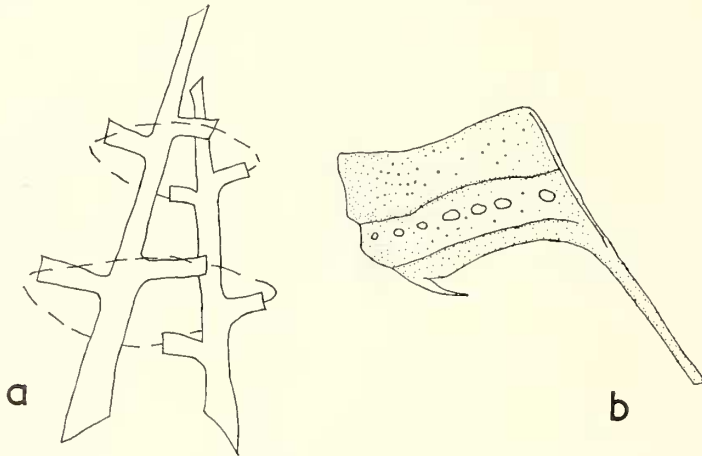
Winged nassellinid, Holdsworth 1964, p. 698.

Locality. Upper Dove Valley, South-west Derbyshire, England.

Horizon. Faunal band of *Reticuloceras paucirenulatum*, *Reticuloceras circumplicatile* Zone (R_{1a}), Kinderscoutian Stage (R₁), Namurian Series, Carboniferous.

Diagnosis. The shell bears prominent dorsal and ventral wings developed in a single plane, is conical from apex to the level of emergence of the wings, and tubular thereafter. In the most typical form the tubular portion of the shell constitutes about one-third of the total length, the overall outline being essentially triangular, but elongate variants occur in which the tubular portion may constitute half the length of the shell. Slightly oblique transverse constrictions divide the shell into segments and nine segments can be detected in complete specimens, though the first three are small and indistinct. A slender, slightly curved apical spine, hollow at the base, is developed from the first segment and there is generally a sudden increase in width of the lattice shell at the fourth segment. The wings arise most commonly at or about the level of the sixth segment and usually bear weak, longitudinal wing ribs, sometimes produced into wing spines. There is a general tendency for the dorsal wing to be developed slightly nearer the apex than the ventral wing. Both longitudinal rods of the H-frame continue into the shell interior as columellae, lying in the plane of the wings. The columellae are of markedly dissimilar strength, the stronger (dorsal) arising from the stronger rod of the H-frame. The columellae converge towards the apex of the shell, extending at least to the third segment and possibly to the apical segment. Along their entire length both columellae are attached to the adjacent lattice wall by pairs of small lateral branches (trabeculae), members of a pair being slightly offset vertically. The branches contact

the lattice shell at the constrictions (text-fig. 2*a*), and commonly there is indication of slight thickening of the shell along the apical sides of constrictions. The lattice shell is imperforate except for the final segment, where a girdle of irregular pores may be developed close to the constriction (text-fig. 2*b*). The transverse bar of the H-frame, only very rarely preserved completely in the available material, is slightly curved and ornamented with short spines (text-fig. 1*b*).



TEXT-FIG. 2. *Alibaillella pennata* sp. nov.

a, Diagram showing relationship between constrictions of lattice shell (dashed lines) and trabeculae of the internal columellae.

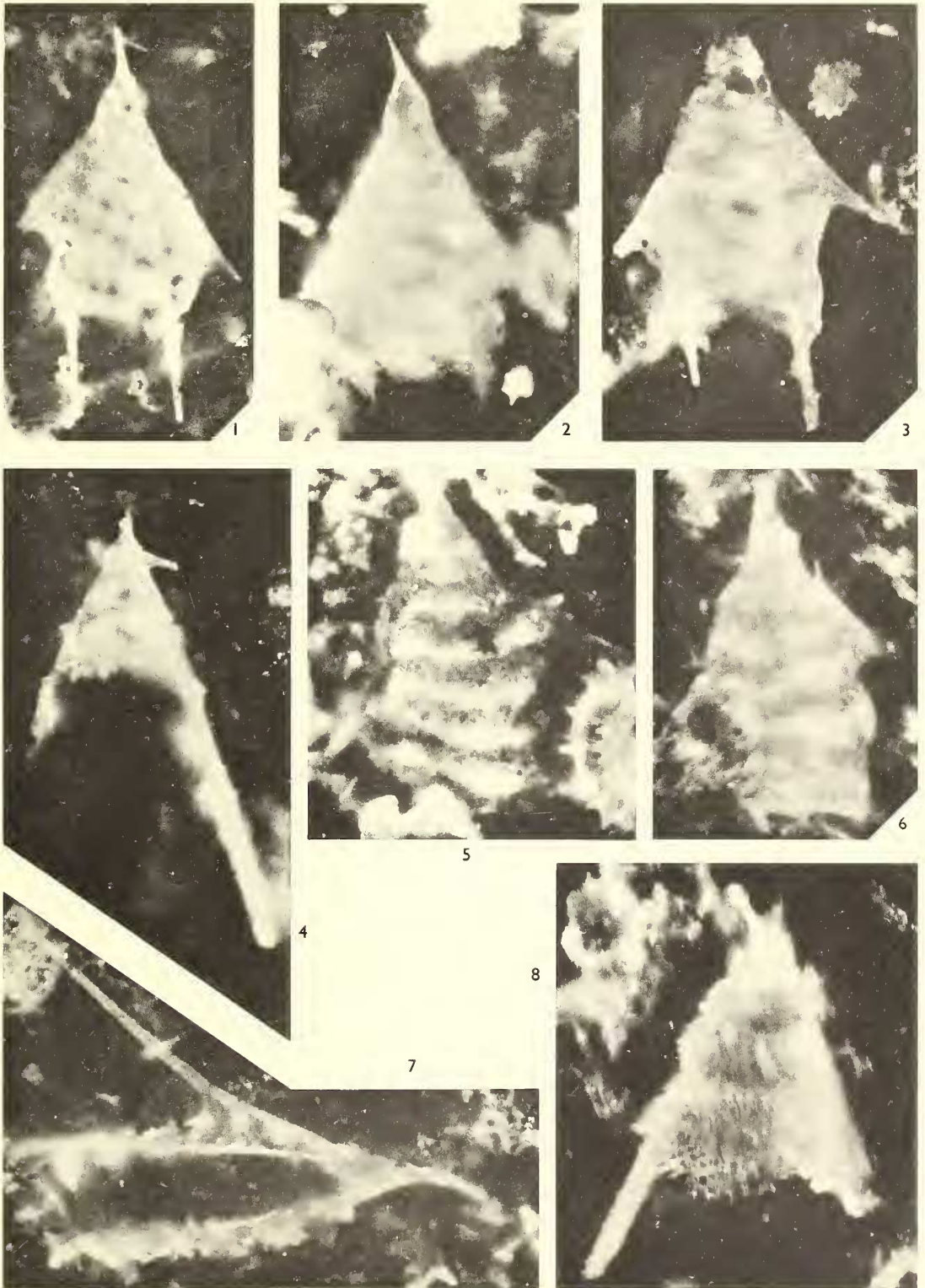
b, Final and penultimate segments with portion of dorsal rod of H-frame, showing girdle of irregular pores in final segment. Drawing from specimen, $\times 250$.

Variation. Specimens assigned to *A. pennata* are somewhat variable. The most distinct variant is an elongate form in which the tubular portion of the shell is up to half the total shell length and the wing spines are very long, extending to or beyond the level of the mouth. In the typical triangular form there is variation in the degree to which the segments are defined, in the development of wing ribs and wing spines, and in the size and position of the wings. In an extremely rare variant the development of the ventral

EXPLANATION OF PLATE 54

All figures $\times 250$.

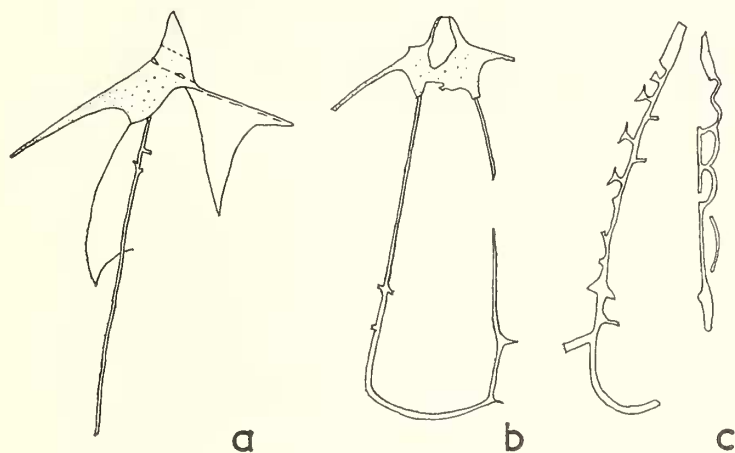
Figs. 1–3, 5–7. *Alibaillella pennata* sp. nov. 1, Holotype, LZ 3651. 2, Topotype, LZ 4740, showing segmentation and incomplete apical spine. 3, Topotype, LZ 4739, showing marked inequality in strength of rods of H-frame and difference in level of the wings. 5, Paratype, LZ 3652, showing very well-marked segmentation. 6, Topotype, LZ 4737, elongate form showing segmentation and portion of wing spine. 7, Paratype, LZ 3653, elongate form with wing rib produced into long wing spine. Figs. 4, 8. *Popofskyellum undulatum* Deflandre. 4, Very incomplete specimen showing one lateral cephalic spine and the stronger of the two longitudinal ribs, LZ 4738. 8, Specimen showing the widely conical, segmented lattice of undulose outline, one lateral cephalic spine, and the stronger of the two longitudinal ribs, LZ 4736.



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wing is delayed until the final segment. Occasionally pores are present in both final and penultimate segments, and some specimens lack pores completely.

Material. Deposited at the Geological Survey, Leeds. Holotype, LZ 3651 (Pl. 54, fig. 1), typical triangular form, but with segmentation rather weakly developed; length from tip of apical spine (probably broken) to base of dorsal rod of H-frame 0.24 mm. LZ 3658 is closely comparable with the holotype. Paratype, LZ 3652 (Pl. 54, fig. 5) and LZ 3654 show typical triangular shape with well-developed segmentation. LZ 3657, typical form, laterally broken, showing columellae internally. LZ 3655, triangular form with ventral wing weak, delicately spined and developed closer than usual to mouth. Paratype, LZ 3653 (Pl. 54, fig. 7), extreme elongate form with long wing spine; length from tip of apical spine (probably broken) to damaged aperture 0.31 mm. LZ 3656, specimen with shape intermediate between typical and elongate forms, having very weak ventral wing with strong, curved spine. Specimens cited are on the etched surfaces of two small slabs of limestone, and detailed instructions for locating specimens are deposited with the material. Figured specimens not cited above also have Geological Survey, Leeds, registration numbers.



TEXT-FIG. 3. *Alibaillella* aff. *pennata* sp. nov. Drawings from specimens. *a*, Broken specimen showing apex of lattice shell with wings and one internal columella with remnants of trabeculae, $\times 203$. *b*, Broken specimen showing complete H-frame, two internal columellae and wings, $\times 180$. *c*, Broken specimen with only fragments of lattice shell, showing part of H-frame, and two internal columellae bearing remnants of trabeculae, $\times 164$.

Remarks. *A. pennata* differs from the four Viséan species of *Alibaillella* so far described in possessing two wings and a rather markedly segmented shell. It differs also in that specimens invariably show a well-differentiated ventral columella bearing trabeculae.

A. pennata has been seen only at the horizon of *R. paucicremulatum*, but poorly preserved specimens of a closely related form, determined as *A. aff. pennata*, are present at the lower horizon of *Homoceras subglobosum* Bisat. In *A. aff. pennata* (text-fig. 3*a-c*), as in *A. pennata*, there are two columellae, both bearing trabeculae, but the shell is more slender and less obviously segmented, and the two wings are smaller and set more closely to the apex.

Suborder ? NASSELLINA
Family POPOFSKYELLIDAE Deflandre 1964

Diagnosis. Fossil Radiolaria with a perforated, bell-shaped shell in which two opposed, longitudinal, lateral rods are incorporated. Cephalis simple. Podome with two branches.

Remarks. Though the greater part of the shell has a bilateral symmetry Deflandre (1964) excluded the family from the Albaillellina on the grounds that the arrangement of cephalic spines lacks this symmetry. The family differs also in having a perforate shell and lacking internal columellae, the longitudinal ribs being integral parts of the shell, homologous with the wing ribs of *A. pennata*. In the Namurian examples seen these longitudinal ribs or rods are of unequal strength.

Genus POPOFSKYELLUM Deflandre 1964

Type species. *Popofskyellum pulchrum* Deflandre (1960, pl. 1, fig. 26).

Diagnosis. Shell perforated, bell-shaped or conical, with two opposed lateral ribs or rods, usually projecting at the base. Podome with two branches. Cephalis with unbranched spines, frequently with a short, conical, tricostate spine. Poorly known, asymmetrical trabecular system basally.

Popofskyellum undulatum Deflandre

Plate 54; figs. 4, 8

Popofskyellum undulatum Deflandre 1964, pp. 3055-8; figs. 3, 4, 13, 14.

Remarks. All five incomplete Namurian specimens of the genus so far seen agree closely in size and architecture with *P. undulatum*, described by Deflandre from the Viséan. The most complete specimen (Pl. 54; fig. 8) has a cephalis and five other rather well-marked segments as in the holotype (cf. Deflandre 1964, fig. 14), giving the characteristic undulose outline to the shell, which is finely perforated overall and of muslin-like texture. The longitudinal rods of unequal strength arise in the region of the second extra-cephalic segment and extend beyond the periphery of the mouth. The total number of lateral cephalic spines cannot be determined, but there is at least one per specimen, and also a slender apical spine.

Popofskyellum is very rare in the Namurian faunas studied, being seen only at the horizon of *R. paucicrenulatum*, where it is associated with abundant specimens of *A. pennata*. The genus also appears to be rare in the Viséan faunas, for Deflandre's four species are based on a total of only about twenty specimens (Deflandre 1964, p. 3055).

ECOLOGY OF ALBAILLELLA PENNATA

Foreman (1963, p. 267) noted marked differences in relative abundance and morphology of radiolarian species between three concretions studied, all collected at 'approximately the same horizon' and separated by a total horizontal distance of only some four miles. The radiolarian faunas of the *R. paucicrenulatum* faunal band provide an even more striking example of apparent lateral variation at a single horizon.

The band was studied at three localities. At locality 1 in the Upper Dove Valley (loc. 179 of Holdsworth 1963) two bullions with *R. paucicrenulatum*, at exactly the same level, 1 foot apart horizontally, contained rich spumelline faunas abundantly associated with *A. pennata* and with very rare *P. undulatum*. Both these forms were completely absent from a bullion with the same goniatite at locality 2, 20 yards away and also from a fourth bullion with the goniatite at locality 3, 1 mile away in the Upper Manifold Valley (loc. 177 of Holdsworth 1963), which contained a rich but exclusively spumelline fauna. The possibility that the bullions at the three different localities are parts of three, vertically separated goniatite bands is remote. The goniatites present in all four collections are typical forms of *R. paucicrenulatum* (Holdsworth 1963, pp. 142–4) and in no known succession is this species seen to occur more than once. It must be accepted that the four bullions consist of sediment deposited during the single relatively brief time span marked by the existence in the area of *R. paucicrenulatum*.

This is not to say, however, that the two bullions from locality 1 and those from localities 2 and 3 constitute precisely contemporaneous sediment samples, even though the majority of faunal bands in this portion of the succession average only a foot or so in thickness. From the perfect three-dimensional preservation of goniatites in bullions it is clear that these concretions grew very early in diagenesis, before the oozes and muds had suffered any appreciable compaction. To judge by the total crushing of many globose goniatites in Namurian shale bands, an inch of shale must represent many inches of original sediment, and at the time the bullion concretions formed it seems probable that many inches, even feet, of highly water-charged mud and ooze were present below the sediment-water interface. As the *R. paucicrenulatum* bullions are relatively small, approximately seven inches deep at maximum, it is possible that the two bullions of locality 1 and those of localities 2 and 3 developed at three slightly different levels in the single sheet of sediment containing *R. paucicrenulatum*.

Thus there is a high probability that the variation between faunas at the three localities is a vertical, not a true lateral, variation. During the single time span marked by the existence of *R. paucicrenulatum* there were probably at least two distinct periods, one in which *A. pennata* coexisted abundantly with the goniatite and spumelline Radiolaria, and one in which only the goniatite and spumellines were present in the area.

To suppose that this indicates an extremely brief stratigraphical range for *A. pennata* is unrealistic in view of the evidently long ranges of the spumelline species and the presence of the closely comparable *A. aff. pennata* at a single lower horizon. The most reasonable explanation is that the occurrence of *A. pennata* was controlled by environment, and it is significant that *Popofskyellum* occurs only in association with *A. pennata*. Though probably not closely related phylogenetically, there are obvious similarities between the conical, bilaterally symmetrical genera *Albaillella* and *Popofskyellum*, and Deflandre (1964, p. 3057) suggested an evolutionary convergence in morphology. If the appearance of *A. pennata* was due to environmental change, then we must suppose, in view of the rarity of faunas including *Albaillella*, that the change taking place during '*R. paucicrenulatum* time' was somewhat unusual in the histories of the goniatite bands of Derbyshire and Staffordshire.

In considering the nature of this change it is significant that whilst *A. pennata* is extremely abundant in the bullions of locality 1, all the common spumellines of other horizons are also present in considerable numbers. The change in environment had no